Nutritional Ecology of the Formosan Subterranean Termite (Isoptera: Rhinotermitidae): Growth and Survival of Incipient Colonies Feeding on Preferred Wood Species

JUAN A. MORALES-RAMOS[1] AND M. GUADALUPE ROJAS

USDA-ARS, Southern Regional Research Center, Formosan Subterranean Termite Research Unit, New Orleans, LA 70124

J. Econ. Entomol. 96(1): 106–116 (2003)

ABSTRACT The wood of 11 plant species was evaluated as a food source significantly impacting the growth and survival of incipient colonies of the Formosan subterranean termite, *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae). Colonies of *C. formosanus* feeding on pecan, *Carya illinoensis* (Wangenh.), and red gum, *Liquidambar styraciflua* L., produced significantly more progeny than colonies feeding on other wood species tested. Progeny of colonies feeding on pecan and American ash, *Fraxinus americana* L., had significantly greater survival than progeny of colonies feeding on other wood species. Colonies feeding on a nutritionally supplemented cellulose based matrix showed similar fitness characteristics as colonies feeding on the best wood treatments. These results indicate that differences observed in colony fitness can be partially explained by nutritional value of the food treatment, raising the possibility that wood from different tree species have different nutritional values to the Formosan subterranean termites. Colonies feeding on loblolly pine, *Pinus taeda* L., and ponderosa pine, *Pinus ponderosa* Laws., had significantly lower survival and produced significantly fewer workers and soldiers than colonies feeding on other wood species. Colony survival from 90 to 180 d of age and from 90 to 360 d of age was significantly correlated with the number of workers present at 90 d of colony age, indicating that colony survival depends on the presence of workers. Wood consumption in a multiple-choice study was significantly correlated with colony fitness value. This suggests that feeding preference of *C. formosanus* is at least partially influenced by the nutritional value of the food source.

KEY WORDS *Coptotermes formosanus*, incipient colonies, nutrition, reproduction, wood species

THE FORMOSAN SUBTERRANEAN termite, *Coptotermes formosanus* Shiraki, has been one of the most destructive termites in the continental United States (Beal 1987). It is estimated that the Formosan subterranean termite causes damage of several millions of dollars annually (Su and Tamashiro 1987, Su and Scheffrahn 1990) to houses, other buildings, utility poles, railway sleepers, boats and ships, paper, and living trees (Edwards and Mill 1986). The Formosan subterranean termite was first detected in the continental United States in Houston, TX in 1965 and in 1967 was also detected in Galveston, TX, Charleston, SC, New Orleans, LA, and Lake Charles, LA (Beal 1987). By 2001, The Formosan subterranean termite had spread to 95 counties in 11 states including Alabama, California, Florida, Georgia, Hawaii, Louisiana, Mississippi, North Carolina, South Carolina, Tennessee, and Texas (Woodson et al. 2001).

Among the newest and more effective control methods for the Formosan subterranean termite is the use of in-ground slow-acting toxic baits (Su 1991; Su and Scheffrahn 1993, 1996). Termite baits deliver toxicants via ingestion, and their effectiveness depends upon the consumption of the bait by the termites (Grace et al. 1996, Henderson and Forschler 1996). Consumption of a particular food source is often determined by feeding preferences when a diversity of food sources is available (Morales-Ramos and Rojas 2001). Determining the nature of the feeding preferences of the Formosan subterranean termite may contribute to the improvement of bait consumption by matching bait formulation to the feeding preferences of the Formosan subterranean termite.

Subterranean termites, like many other insects, tend to discriminate when choosing among different species of wood as food. Many studies have reported differences in feeding rates and survival of subterranean termite workers in multiple-choice tests with different species of wood (Smythe and Carter 1970, Mannesmann 1973, Waller et al. 1990, Morales-Ramos and Rojas 2001). Rojas and Morales-Ramos (2001) hypothesized that the Formosan subterranean termite feeding preferences may be determined by the nutritional value of the food source. If this is true, then foraging preferences of the Formosan subterranean

[1] E-mail: jmorales@srrc.ars.usda.gov.

termite could follow optimal foraging theory, which postulates that animals choose their food according to their nutritional needs to optimize fitness (Emlen 1973). By presenting a bait toxicant to an insect within an optimal food source, the probability of consumption of the toxicant could be increased.

The objectives of this study were to determine the nutritional value of some of the most preferred wood species by the Formosan subterranean termite by comparing growth and survival of incipient colonies and to measure the correlation between nutritional value and relative preference of wood species to the Formosan subterranean termite.

Materials and Methods

Collection and Colony Preparation. Alates of the Formosan subterranean termite were collected using an ultraviolet light trap. The trap was located at the Northwest end of the SRRC campus bordering New Orleans City Park (Louisiana). The trap was equipped with a timer set to turn on at 2000 hours and off at 2300 hours. Three wet paper towels were place inside the main container of the trap to aid survival of alates. Collections were made daily starting on 10 May 2000 and ending on 31 July 2000.

Collected alates were placed inside 11.3-liter storage boxes (Rubbermaid Inc., Wooster, OH) with a wet paper towel until they lost their wings, becoming dealates. Dealates were transferred to another box lined inside with a wet paper towel. Almost immediately, dealates formed pairs where males closely followed females.

Hundreds of pairs of reproductive stages were individually placed in 12.4-ml snap-cap plastic vials (Fisher 03–338-3C, Fisher, Pittsburgh, PA) using a vacuum aspirator. A piece of wet paper towel (4 × 4 cm) was placed inside each vial to provide food and water. Vials with termite pairs were kept at 27 ± 1°C, 95 ± 5% RH, and total darkness for 1 wk. Pairs were checked daily for mortality and presence of eggs.

First Stage Experiment. Only pairs that had oviposited were selected to produce incipient colonies. Incipient colonies were produced by placing ovipositing termite pairs in tight-fit lid dishes (9 × 50 mm diameter, Falcon 1006, Fisher, Pittsburgh, PA) with 3 g of a 1:2 mix of wood dust and water. The wood dust was prepared by using a high-speed rotary tool (Multipro 5, Dremel, Racine, WI) equipped with a sanding band (60 grit). Blocks of wood from each of the species were sanded using this rotary tool inside a plastic box to capture the wood dust. The plastic box was washed and dried each time to avoid contamination of wood dust from different species. The wood from all species tested was purchased locally (Riverside Lumber, New Orleans, LA). The eggs were eliminated to allow all termite pairs to start oviposition simultaneously. Pairs collected at a given date were divided evenly among all treatments to control for collection date effects in the analysis.

A total of 11 groups of 60 incipient colonies of the Formosan subterranean termite were provided with a wood dust-water mix from 11 different wood species reported to be preferred by these termites (Morales-Ramos and Rojas 2001). Wood species included in the study are presented in Table 1. A control group was provided with a nutritionally formulated matrix as reported by Rojas and Morales-Ramos (2001). Incipient colonies were kept at 27 ± 1°C, 95 ± 5% RH, and total darkness for the duration of the study. The first stage of the study lasted 6 mo.

Table 1. Wood species tested for nutritional value to *C. formosanus*

Common name	Scientific name
Loblolly pine[a]	*Pinus taeda* L.
Ponderosa pine[a]	*Pinus ponderosa* Laws.
Douglas fir[a]	*Pseudotsuga menziesii* (Mirb.)
Sugar maple[b]	*Acer saccharum* Marsh.
American ash[b]	*Fraxinus americana* L.
Pecan[b]	*Carya illinoensis* (Wangenh.)
Yellow poplar[a]	*Liriodendron tulipifera* L.
Trembling aspen[b]	*Populus tremuloides* Michx.
Red gum, sweetgum[b]	*Liquidambar styraciflua* L.
Northern red oak[b]	*Quercus rubra* L.
Yellow birch[b]	*Betula alleghaniensis* Britton
Nutritionally supplemented matrix	

All wood species originated from two separate wood boards (per species) purchased with at least 2 months of difference.
[a] Mostly sapwood.
[b] Both sapwood and heartwood.
[c] Mostly heartwood.

Incipient colonies were monitored every 15 d to count progeny and record mortality of pairs during the first 3 mo. During the following 3 mo, pairs were monitored monthly for mortality only. At the end of the 6-mo period, the dishes containing the incipient colonies were opened to count progeny. Total number of eggs, immature stages, workers, and soldiers were recorded for each incipient colony.

Second Stage Experiment. Special arenas were constructed to house the incipient colonies for the second stage of the study. The arenas consisted of two plastic tight-fitting lid dishes (9 × 50 mm diameter) stacked and glued with all purpose hot glue (Product No. BAP5–4, Arrow Fastener Co. Inc., Saddle Brook, NJ). The two dishes were connected vertically in the center by a 5-mm diameter hole. The bottom dish was filled with a 1:1 mix of play sand and topsoil (passed trough a No. 16 sieve). De-ionized water was added totaling 30% of the mix. The top dish was used as a foraging area where 1 g of 1-mm thick wood pieces were placed. The wood provided was of the corresponding species for each treatment.

At the end of the first stage, termite pairs with all their progeny were transferred to the new arenas. Termites were removed from the tight-fit lid dishes and placed on the top dish of the new arenas. Termites migrated to the bottom dish within 2 d by digging tunnels in the soil mix. Control colonies were provided with 3 g of the nutritional mix; no soil was provided. The pairs were held at the environmental conditions described above for an additional 6 mo. Colonies were

monitored monthly for mortality. At the end of the second 6-mo period (1 yr) the dishes were opened to count the progeny from each incipient colony. Total number of eggs, immature stages, workers, and soldiers were recorded.

Data Analysis. The mean number of eggs, larvae, and workers and soldiers were compared between treatments by two methods. The first method was analysis of variance (ANOVA) and Student *t*-test of paired means. The second method was the contrast option of the general linear model (GLM) procedure of JMP software (SAS Institute 1995). Comparisons of number of eggs, larvae, and workers and soldiers were made at 60, 90, 180, and 360 d of colony age. Colony growth was measured as the number of workers and soldiers present at any given colony age. Number of eggs was also compared at 30 d of colony age. Changes in the number of eggs and larvae were considered less important as measures of colony growth because frequent cannibalizing of these stages was observed throughout the study.

The survival of incipient colonies was measured by calculating the proportion of surviving colonies at a given age. The proportion of surviving colonies was called survival rate and had values from 0 (0% survival) to one (100% survival). Survival rates of incipient colonies of the different treatments were compared using the Z-test for categorical data (Ott 1984). Colony survival was compared at 60, 90, 180, and 360 d of colony age.

The product of colony survival rates and the number of workers and soldiers (colony growth) was calculated as a measure of colony fitness (*Cf*). This value mimics the L_xM_x value called net maternity used in fertility tables to estimate rates of population increase (Carey 1993); however, in this case *Cf* does not reflect the population rate of increase because progeny of the Formosan subterranean termite is nonreproductive during the early stages of colony growth. A modification of the Tukey jackknife technique (Tukey 1958, Roff 1992) was used to generate 30 estimates of colony fitness per treatment. These 30 fitness values were calculated by deleting 10 randomly selected data points from the data set ($n = 60$) and restoring the data set after calculation of colony fitness, as described by Rojas et al. (1999). This procedure was repeated 30 times to obtain 30 different estimates of colony fitness. ANOVA and Student *t*-test of paired means were used to compare colony fitness between wood treatments.

Total number of eggs oviposited per colony (queen fecundity) during the first stage of the experiment was estimated from the egg count data taken at 15-d intervals using the Kiritani and Nakasuji graphic integration method modified by Manly (1976) to estimate numbers entering stage. This method calculates total numbers of a given stage by integrating observed densities at different time intervals measured in developmental rates (Manly 1976). The formula takes the form:

$$AH = \tfrac{1}{2}\sum_{i=1}^{n}(h_i + h_{i+1})\,E_i$$

for

$$h_i = DR_i - DR_{i-1}$$

where AH is the total area under the curve, E_i is the mean number of termite eggs per colony at date i, DR is the accumulated developmental rates at date i, and n is the last sample date. Because Formosan subterranean termite colonies were kept at constant 27 ± 1°C, developmental rates were calculated as 1/developmental time at 27 ± 1°C. Developmental time of Formosan subterranean termite eggs at 27 ± 1°C was determined by doing daily observations of the incipient colonies during this study. Mean developmental time of *C. formosanus* eggs was 35 d at this temperature.

Progeny survival was calculated as the proportion of eggs successfully completing development from egg to worker (fourth instar) or presoldier (fourth instar). Number of workers, presoldiers, and soldiers observed at 180 d of colony age was divided by the estimated number of eggs oviposited to 100 d of age. Progeny survival was compared by Z-test as colony survival.

Simple linear regression was used to analyze the relationship between incipient colony fitness in a preferred wood species and the mean consumption rate of the same wood species by termite groups (2,500) in a multiple-choice test as reported by Morales-Ramos and Rojas (2001). Simple linear regression was also used to relate colony survival rate and number of workers present per colony for each wood species.

Results

Overall Growth and Survival of Incipient Colonies. At 27 ± 1°C, new batches of eggs were first observed 15 d after the pairs were transferred. Larvae were first observed at day 45, workers and soldiers were first observed at day 60 (Fig. 1). The peak oviposition occurred between 30 and 45 d of colony age.

Overall means of total observed progeny comprising all wood treatments were 23.3 ± 0.8, 18.0 ± 0.8, 15.2 ± 0.78, and 33.1 ± 1.99 at 60, 90, 180, and 360 d of colony age, respectively. Means of hatched progeny observed were 9.4 ± 0.4, 11.9 ± 0.6, 14.2 ± 0.79, and 30.9 ± 1.81 at 60, 90, 180, and 360 d of colony age, respectively. Means of observed workers and soldiers were 2.6 ± 0.16, 8.4 ± 0.42, 13.9 ± 0.79, and 28.4 ± 1.63 at 60, 90, 180, and 360 d of colony age, respectively (Table 2).

Mean estimated total eggs oviposited per pair (colony) at age of 105 d was 36.8 ± 1.03 (Table 2). The greatest mean number of eggs observed occurred at 45 d and was 16.2 ± 0.5. The maximum number of eggs observed was 50 and occurred at 45 d of age in the supplemented matrix treatment. Overall colony survival was 45.3 ± 4.2, 36.5 ± 3.9, and 20 ± 2.6% at 90, 180, and 360 d (Table 2).

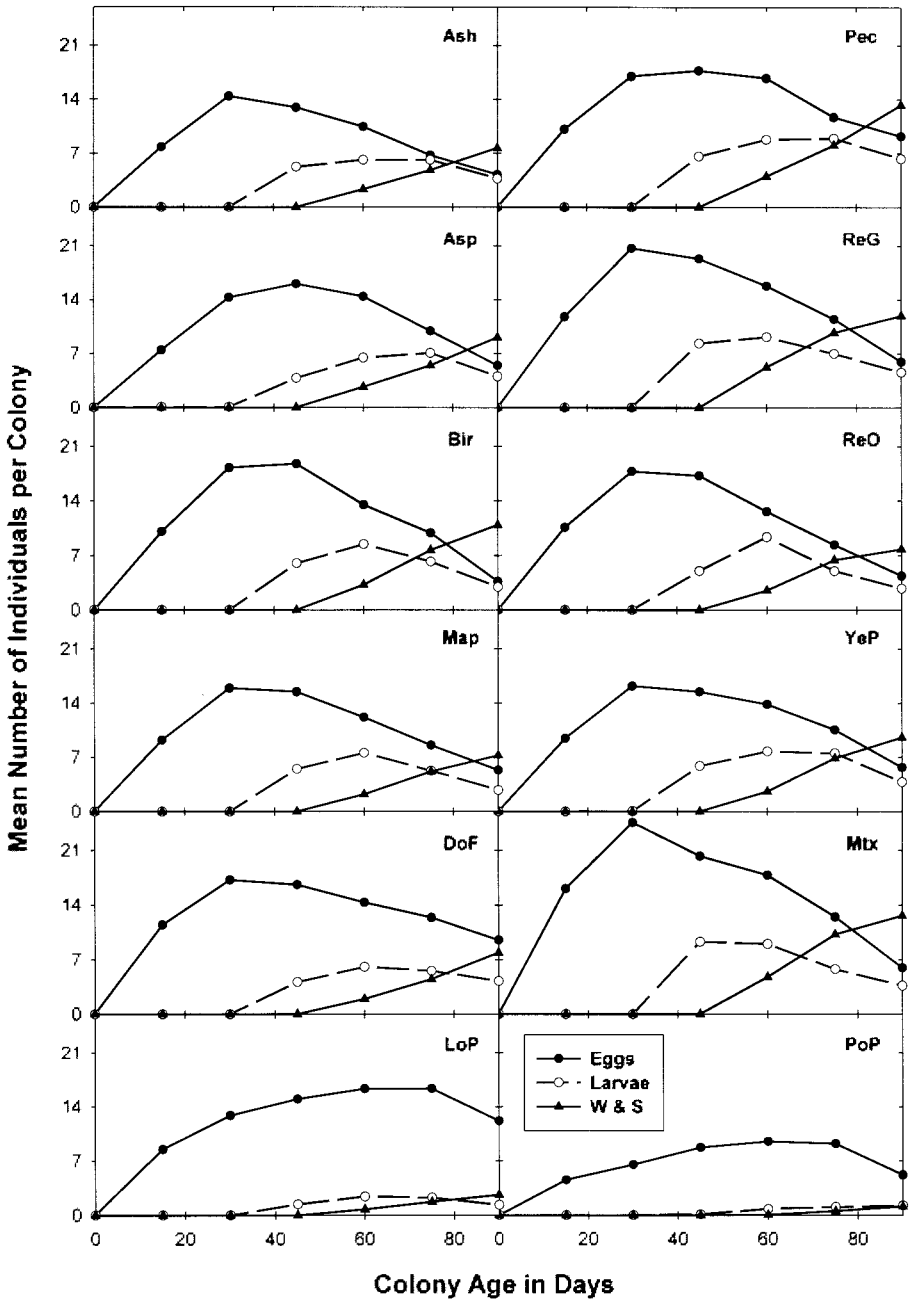

Fig. 1. Stage distribution of Formosan subterranean termite incipient colonies feeding on 11 wood species and a nutritionally supplemented matrix during the first 90 d after establishment. Three letter keys are defined in Table 1.

Food Treatment Effect on Colony Growth. Differences in growth and survival among the colonies fed with different wood species were statistically significant. However, there were few significant differences in the number of eggs observed between the different treatments at 30, 60, 90, 180, and 360 d. Colonies fed with the nutritionally supplemented matrix oviposited significantly more eggs than the rest of the treatments at 30 d (contrast $F = 38.31$; df = 1, 391; $P < 0.0001$) and 360 d (contrast $F = 37.11$; df = 1, 118; $P < 0.0001$) of age (Table 3). Colonies fed on ponderosa pine oviposited significantly fewer eggs than the rest of the treatments at 30 d (contrast $F = 60.67$; df = 1, 391; $P < 0.0001$) and 45 d (contrast $F = 20.93$; df = 1, 356; $P < 0.0001$) of age.

Most treatments showed no significant difference in the total number of eggs (queen fecundity) estimated by the graphic method, but, pairs reared on ponderosa

Table 2. Overall means of some biological parameters observed on *C. formosanus* incipient colonies fed on 11 wood species and a nutritionally supplemented matrix

Parameter	Age in d	*n*	Mean	SEM
Observed eggs				
	30	403	16.12	0.443
	45	368	16.15	0.500
	60	344	13.92	0.514
	90	302	6.19	0.438
	180	243	1.06	0.232
	360	130	2.19	0.332
Total eggs[a]	105	229	36.79	1.027
Percent progeny survival[b]	180	229	38.46	1.874
Observed larvae[c]				
	60	344	6.78	0.291
	90	298	3.38	0.227
	180	243	0.21	0.063
	360	130	2.51	0.287
Observed workers and soldiers[d]				
	60	344	2.64	0.155
	90	302	8.44	0.424
	180	243	13.94	0.792
	360	130	28.39	1.633
Soldier percentage				
	90	12	7.49	0.427
	180	12	12.45	0.526
	360	12	14.38	0.547
Total progeny observed				
	60	344	23.34	0.797
	90	302	18.01	0.790
	180	243	15.21	0.777
	360	130	33.09	1.993
Percent colony survival				
	90	12	45.28	4.153
	180	12	36.46	3.931
	360	12	20.00	2.556

n = number of live colonies, SEM = standard error of the mean.
[a] Calculated by Kiritani and Nakasuji's graphic integration method from egg counts at 15-d intervals from 0 to 90 d of age.
[b] Workers and soldiers at age 180 d divided by total eggs estimated by graphic method.
[c] First, second, and third instars.
[d] Forth instars and older.

pine produced significantly fewer eggs than the rest of the treatments ($F = 29.74$; df = 1, 217; $P < 0.0001$) except ash (Table 4). Graphic distribution of eggs, larvae, and workers and soldiers during the first 90 d was similar in most of the treatments except in the ponderosa pine and loblolly pine treatments (Fig. 1). Colonies fed on these two treatments showed reduced numbers of emerged progeny (larvae, workers, and soldiers) and a more continuous oviposition pattern (Fig. 1).

Colonies feeding on the supplemented matrix, red gum, and pecan had significantly more workers and soldiers than the rest of the treatments at age 60 d ($F = 60.98$; df = 1, 332; $P < 0.0001$) and age 90 d ($F = 34.18$; df = 1, 290; $P < 0.0001$). No significant differences were observed among these three treatments in the number of workers and soldiers at these two ages (Table 3). Colonies feeding on loblolly pine and ponderosa pine showed significantly fewer workers and soldiers than the rest of the treatments at the same two ages ($F = 53.85$ and 55.13; df = 1, 332 and 1, 290; $P < 0.0001$) (Table 3). The rest of the treatments showed no significant differences among each other in the mean number of workers and soldiers at ages 60 and 90 d.

At 180 d of age, colonies feeding on pecan had significantly more workers and soldiers than the rest of the treatments ($F = 37.39$; df = 1, 231; $P < 0.0001$). At this same age, colonies feeding on ponderosa pine produced significantly fewer workers and soldiers than the rest of the treatments ($F = 15.96$; df = 1, 231; $P < 0.0001$). No significant differences in the number of workers and soldiers were observed among the other treatments at this age (Table 3).

The pecan and supplemented matrix treatments produced significantly more workers and soldiers than the rest of the treatments at 1 yr of colony age ($F = 50.11$; df = 1, 118; $P < 0.00001$) showing the highest colony growth at this age.

Food Treatment Effect on Survival. The aspen treatment had significantly greater colony survival than the rest of the treatments at 60, 90, and 180 d of age (Table 3). Mortality increased substantially in the aspen treatment between 180 and 360 d of age (Fig. 2). The opposite was observed in the pecan and yellow poplar treatments, which showed the least colony survival at 60 d of age and were significantly less than the rest of the treatments ($Z > 1.96$). However, mortality sharply declined after age 45 d (Fig. 2) in the pecan and yellow poplar treatments and colony survival in these two treatments was not significantly different than that of most of the other treatments at 360 d of age (Table 3). Colony survival at 1 yr of age ranged from 6.7% in loblolly pine to 33.3% in Douglas fir. Differences in survival at 360 d of age were significant only between the best three (Douglas fir, aspen, and red gum) and the worst three (ash, ponderosa pine, and loblolly pine) treatments ($Z > 1.96$) (Table 3; Fig. 2). Survival during the early colony stages was greatly affected by the treatments, but differences in colony survival decreased with colony age.

A multiple general linear model analysis of colony survival between 90 and 360 d of age with two independent variables showed that food treatment had no significant effect on colony survival. However, number of workers per colony at 90 d of age had a highly significant effect on colony survival during the following 3 mo ($F = 95.96$; df = 1, 289; $P < 0.0001$). The mean number of workers observed at 90 d of colony age were significantly greater in colonies that survived to 360 d than in colonies that died before 180 d of age ($T = 10.32$, df = 173, $P < 0.0001$) within most of the treatments (Table 5). Similarly, mean number of workers observed at 180 d of age were significantly greater in colonies surviving to 360 d of age than in colonies dying between 180 and 360 d of age ($T = 10.14$, df = 241, $P < 0.0001$) within most of the treatments (Table 5). A significant linear relationship was observed between probability of a colony surviving from 90 to 180 d and the mean number of workers per colony at 90 d of age ($R^2 = 0.52$; $F = 10.81$; df = 1, 10; $P = 0.0082$). Probability of colony survival from 90 to 360 d of age was also significantly correlated with the mean number of workers per colony at 90 d of age ($R^2 = 0.517$; $F = 10.71$; df = 1, 10, $P = 0.0084$) (Fig. 3).

Table 3. Progeny observed in incipient *C. formosanus* colonies of three different ages fed on 11 preferred wood species and a nutritionally supplemented matrix

Wood species	*n*	Eggs[a]	Workers and soldiers[a]	Colony survival[b]	Colony fitness[c]
60 days					
Red gum	30	15.80 ± 2.00ab	5.27 ± 0.66a	0.500d	2.64
Matrix	28	17.82 ± 2.04a	4.75 ± 0.58a	0.518d	2.46
Pecan	18	16.78 ± 2.17ab	4.00 ± 0.64ab	0.308e	1.23
Aspen	37	14.41 ± 1.30abc	2.68 ± 0.32bcd	0.860a	2.30
Birch	30	13.50 ± 1.51abcd	3.23 ± 0.52bc	0.508d	1.64
Poplar	19	13.84 ± 2.48abcd	2.58 ± 0.54bcd	0.317e	0.82
Douglas fir	43	14.33 ± 1.61abc	1.95 ± 0.43de	0.717b	1.40
Maple	31	12.16 ± 1.69bcd	2.19 ± 0.45cd	0.517d	1.13
Red oak	27	12.63 ± 1.56bcd	2.52 ± 0.49bcd	0.458d	1.15
Ash	26	10.42 ± 1.17cd	2.31 ± 0.47cd	0.450d	1.04
Loblolly pine	27	16.33 ± 1.94ab	0.74 ± 0.34e	0.450d	0.33
Ponderosa pine	28	9.46 ± 1.75d	0.04 ± 0.04e	0.467d	0.02
90 days					
Red gum	30	5.93 ± 1.10bcd	11.93 ± 1.32ab	0.500b	5.97 ± 0.08c
Matrix	27	5.93 ± 1.37bcd	12.63 ± 1.60a	0.500b	6.32 ± 0.10b
Pecan	14	9.21 ± 1.83abc	13.29 ± 1.57a	0.242d	3.22 ± 0.06g
Aspen	35	5.46 ± 1.39cd	9.09 ± 1.09bcd	0.826a	7.51 ± 0.07a
Birch	26	3.65 ± 0.95d	10.92 ± 1.42abc	0.442bc	4.83 ± 0.06d
Poplar	18	5.67 ± 1.41bcd	9.56 ± 1.80abcd	0.300d	2.87 ± 0.07h
Douglas fir	28	9.50 ± 1.85ab	7.89 ± 1.31cd	0.492b	3.88 ± 0.06e
Maple	29	5.31 ± 1.23cd	7.24 ± 1.28d	0.500b	3.62 ± 0.07f
Red oak	24	4.38 ± 1.10cd	7.79 ± 1.37cd	0.425bc	3.31 ± 0.06g
Ash	25	4.20 ± 1.00d	7.64 ± 1.25cd	0.433bc	3.31 ± 0.05g
Loblolly pine	21	12.14 ± 2.50a	2.57 ± 1.09e	0.350cd	0.90 ± 0.031
Ponderosa pine	25	5.16 ± 1.67cd	1.08 ± 0.62e	0.425bc	0.46 ± 0.02j
180 days					
Red gum	27	1.37 ± 0.98ab	18.22 ± 2.93b	0.450b	8.20 ± 0.14a
Matrix	23	1.22 ± 0.63ab	18.26 ± 3.57b	0.436b	7.96 ± 0.17b
Pecan	11	0.73 ± 0.49ab	33.82 ± 3.21a	0.208e	7.03 ± 0.14c
Aspen	29	0.72 ± 0.53b	12.21 ± 1.82cd	0.698a	8.52 ± 0.09a
Birch	26	1.00 ± 0.92ab	12.35 ± 2.10bcd	0.433b	5.35 ± 0.09d
Poplar	12	0.83 ± 0.75ab	14.75 ± 2.61bcd	0.200e	2.95 ± 0.08h
Douglas fir	22	1.14 ± 0.60ab	12.77 ± 1.48bcd	0.383bc	4.89 ± 0.08ef
Maple	22	0.41 ± 0.33b	12.23 ± 2.39bcd	0.375bc	4.59 ± 0.08f
Red oak	20	0.15 ± 0.15b	10.00 ± 2.10cde	0.333bcd	3.33 ± 0.07g
Ash	19	1.00 ± 0.79ab	16.16 ± 2.09bc	0.325bc	5.25 ± 0.09e
Loblolly pine	14	3.36 ± 1.76a	8.29 ± 1.94de	0.233de	1.93 ± 0.05i
Ponderosa pine	18	1.39 ± 0.95ab	4.39 ± 2.04e	0.300cde	1.32 ± 0.05j
360 days					
Red gum	18	2.28 ± 1.04b	37.78 ± 4.24ab	0.300abc	11.33 ± 0.22a
Matrix	10	8.60 ± 2.51a	49.00 ± 10.12a	0.200cd	9.80 ± 0.25b
Pecan	10	1.60 ± 0.75b	49.60 ± 3.94a	0.175de	8.68 ± 0.12c
Aspen	12	1.75 ± 0.60b	28.50 ± 2.54bc	0.326ab	9.29 ± 0.19c
Birch	14	0.93 ± 0.44b	25.86 ± 4.40cd	0.242abcd	6.26 ± 0.12d
Poplar	9	1.00 ± 0.44b	30.33 ± 2.76bc	0.150de	4.55 ± 0.14g
Douglas fir	19	1.89 ± 0.58b	17.21 ± 1.68d	0.333a	5.73 ± 0.10e
Maple	11	1.45 ± 0.65b	27.36 ± 4.22bcd	0.200cd	5.47 ± 0.11f
Red oak	12	1.17 ± 0.60b	18.25 ± 3.72cd	0.208bcd	3.80 ± 0.09h
Ash	5	2.20 ± 1.43b	12.40 ± 4.95d	0.100ef	1.24 ± 0.05i
Loblolly pine	4	2.00 ± 1.41b	15.00 ± 5.02cd	0.067f	1.01 ± 0.05i
Ponderosa pine	6	2.33 ± 1.31b	13.17 ± 4.66d	0.100ef	1.32 ± 0.05i

[a] Mean ± SEM. Means with the same letter are not significantly different after GLM contrast t-test ($\alpha = 0.05$, $P < 0.001$).

[b] Survival rates calculated as colonies alive divided by total colonies. Survival rates with the same letter are not significantly different after Z-test, $\alpha = 0.05$.

[c] Calculated as the product of mean number of workers + soldiers times colony survival rate. Tukey's jackknife method used to generate 30 estimates per each treatment on colony ages of 90, 180, and 360 d (n = 30). A single estimate was done for 60-d-old colonies.

Evidence of cannibalism was observed in all treatments. Evidence included heads and bodies (with moving appendages) of workers and soldiers that were partially consumed and mandibles being used as construction materials. Incidence of cannibalism was not measured or compared between the treatments. In the ponderosa pine treatment ≈75% of the colonies showed both reproductive castes lacking antennae. This was not observed in any of the other treatments. Pairs lacking antennae were less successful caring for the eggs than pairs with full antennae. Eggs of pairs lacking antennae were spread around the inside of the container while eggs of normal pairs were concentrated and clumped. In microscope observations, reproductive caste lacking antennae had difficulty finding eggs after oviposition.

Some significant differences were observed in progeny survival within colonies to 180 d of age among the treatments ($F = 4.9$; df = 11, 217; $P < 0.0001$). The pecan treatment showed significantly greater progeny

Table 4. Estimated total eggs per colony and progeny survival within the first 180 days of incipient *C. formosanus* colonies fed with 11 wood species and a nutritionally supplemented matrix

Wood species	*n*	Estimated eggs per colony[ab]	Progeny survival[a]
Pecan	11	45.62 ± 4.25a	73.52 ± 5.38a
Ash	19	28.24 ± 2.31cd	58.42 ± 7.35ab
Red gum	23	43.62 ± 2.94a	46.69 ± 5.73bc
Poplar	11	38.81 ± 4.25ab	42.97 ± 4.98bc
Matrix	22	45.45 ± 3.01a	37.75 ± 6.10c
Aspen	29	31.05 ± 2.72bc	38.35 ± 4.49c
Maple	20	33.69 ± 2.94abc	34.65 ± 5.32c
Birch	24	35.61 ± 2.45abc	33.38 ± 4.42c
Douglas fir	20	43.35 ± 3.73a	33.07 ± 4.05c
Red oak	18	35.12 ± 3.33abc	30.73 ± 5.67cd
Loblolly pine	14	41.60 ± 3.77a	29.72 ± 10.97cd
Ponderosa pine	17	20.14 ± 3.42d	14.24 ± 6.68d

[a] Mean ± SEM, means with same letters are not significantly different after ANOVA Student's *t*-test ($\alpha = 0.05$, $P < 0.001$).

[b] Calculated by Kiritani and Nakasuji's graphic integration method from egg counts at 15-d intervals from 0 to 90 d of age.

survival than the rest of the treatments except ash (contrast $F = 23.77$; df = 1, 217; $P < 0.0001$) (Table 4). This treatment had the lowest colony survival rate, but progeny survival within live colonies was the greatest. The ponderosa pine treatment had significantly less progeny survival than all treatments except for loblolly pine and red oak (contrast $F = 20.56$; df = 1, 217; $P < 0.0001$) (Table 4).

Food Treatment and Colony Fitness. Colony fitness was statistically analyzed only at 90, 180, and 360 d of colony age. At the end of 90 d, colonies feeding on aspen had the greatest fitness value followed by those feeding on the supplemented matrix, red gum, birch, Douglas fir, and maple, respectively (Fig. 4; Table 3). Colonies feeding on aspen continued having the greatest fitness value at the end of 180 d, followed by colonies feeding on red gum, supplemented matrix, pecan, and birch, respectively (Table 3). However, at the end of 360 d, colonies feeding on aspen no longer had the greatest fitness values. Instead colonies feeding on red gum had the greatest fitness values followed by colonies feeding on the supplemented matrix, pecan, aspen, and birch, respectively (Table 3). All these differences were statistically significant ($F = 579.6$; df = 11, 348; $P < 0.0001$).

Relative wood consumption rates by *C. formosanus* in a choice test reported by Morales-Ramos and Rojas (2001) were significantly correlated with colony fitness values (Fig. 5). Linear regression models between the natural logarithm of wood consumption rates and fitness values calculated at 90, 180, and 360 d of colony ages had R^2 values of 0.722, 0.543, and 0.518, respectively ($F = 20.76$, 9.49, and 8.59; df = 1, 8; $P = 0.0019$, 0.0151, and 0.019, respectively) (Fig. 5). Aspen and the supplemented matrix were excluded from the analysis because they were not part of the Morales-Ramos and Rojas (2001) study.

Discussion

The stage distribution of the incipient Formosan subterranean termite colonies between 15 and 360 d of colony age resembles that reported by King and Spink (1974, 1975). Estimates of total eggs oviposited per queen during the first 90 d (38.46) were close to those reported by King and Spink (1974) (34). Estimates by Higa (1981); however, were somewhat larger (48). The method to estimate total eggs used by Higa (1981) consisted on the sum of monthly counts of eggs and this may have resulted on a slight overestimation because developmental time of *C. formosanus* eggs exceeds 1 month (36 d) at 26.7°C which is the average

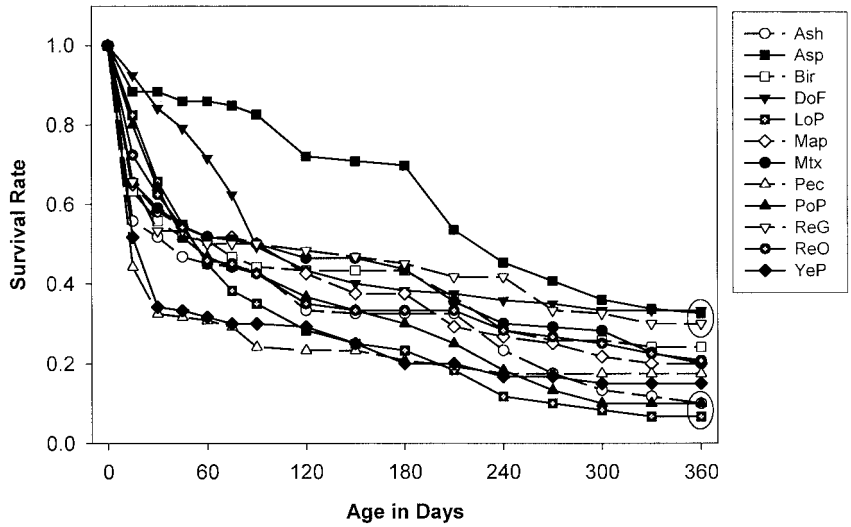

Fig. 2. Survival rates of Formosan subterranean termite incipient colonies fed on 11 wood species and a nutritionally supplemented matrix. Grouping circles show groups of treatments that had significant difference in survival at 1 yr of colony age.

Table 5. Mean number of workers observed in *C. formosanus* incipient colonies surviving to 360 d of age and colonies dying before 180 and 360 d of age

Food treatment	*C. formosanus* colonies		Student *t*-test	df	$P > \|T\|$
	Surviving[a]	Dying[b]			
First analysis: workers at 90 d					
Ash	10.2 ± 2.0	0.8 ± 1.9	3.85*	9	0.0039
Aspen	12.8 ± 1.4	5.2 ± 2.0	2.78*	16	0.0135
Douglas fir	9.1 ± 1.3	1.2 ± 2.3	3.04*	23	0.0058
Maple	11.8 ± 1.7	1.8 ± 1.8	4.17*	16	0.0007
Matrix	16.0 ± 2.1	5.8 ± 3.3	2.95*	12	0.0122
Pecan	13.7 ± 1.3	5.7 ± 2.5	2.87*	11	0.0152
Ponderosa pine	2.8 ± 1.1	0.0	1.62	11	0.1337
Poplar	14.2 ± 1.5	3.5 ± 1.9	4.33*	13	0.0008
Red gum	13.3 ± 1.4	8.0 ± 3.5	1.34	19	0.1960
Red oak	10.5 ± 1.4	1.8 ± 2.5	2.81*	14	0.0140
Loblolly pine	10.5 ± 1.2	0.9 ± 0.9	4.71*	9	0.0011
All	11.6 ± 0.5	2.6 ± 0.7	10.32*	173	<0.0001
Second analysis: workers at 180 d					
Ash	13.2 ± 3.7	14.6 ± 2.2	−0.31	17	0.7571
Aspen	18.3 ± 1.6	5.3 ± 1.3	6.18*	27	<0.0001
Birch	13.6 ± 2.3	7.2 ± 2.5	1.89	24	0.0709
Douglas fir	12.3 ± 1.3	5.3 ± 3.3	1.94	20	0.0661
Maple	19.1 ± 1.7	3.0 ± 1.7	6.60*	20	<0.0001
Matrix	24.9 ± 3.8	8.0 ± 3.3	3.38*	21	0.0029
Ponderosa pine	11.7 ± 2.2	0.0	4.38*	16	0.0005
Poplar	16.0 ± 2.1	4.3 ± 3.7	2.72*	10	0.0214
Red gum	22.4 ± 2.2	2.7 ± 3.1	5.16*	25	<0.0001
Red oak	12.3 ± 1.9	3.3 ± 2.3	2.98*	18	0.0080
Loblolly pine	14.3 ± 2.3	4.7 ± 1.5	3.46*	12	0.0047
All	17.5 ± 0.8	5.9 ± 0.8	10.14*	111	<0.0001

Mean ± SEM. *, Significant difference at $\alpha = 0.05$.
Birch and pecan treatments were not included in the first and second analysis, respectively, for lack of sufficient data.
[a] Colonies surviving to 360 d of age.
[b] Colonies in first analysis dying between 90 and 180 d of age and colonies in the second analysis dying between 180 and 360 d of age.

temperature at which Higa's study was conducted. The graphic method that we used in this study takes into account the developmental time of the eggs. Overall mean of total progeny in our study was 33.09 ± 1.99 ranging from 0 to 122; however, means total progeny ranged among treatments from 65.2 ± 14.12 in the supplemented matrix group to 18 ± 6.16 in the loblolly pine group. Means number of total progeny obtained in our study approached those obtained by King and Spink (1974) (65.5). However, Higa (1981) reported total progeny counts somewhat larger (195) than those observed in our study.

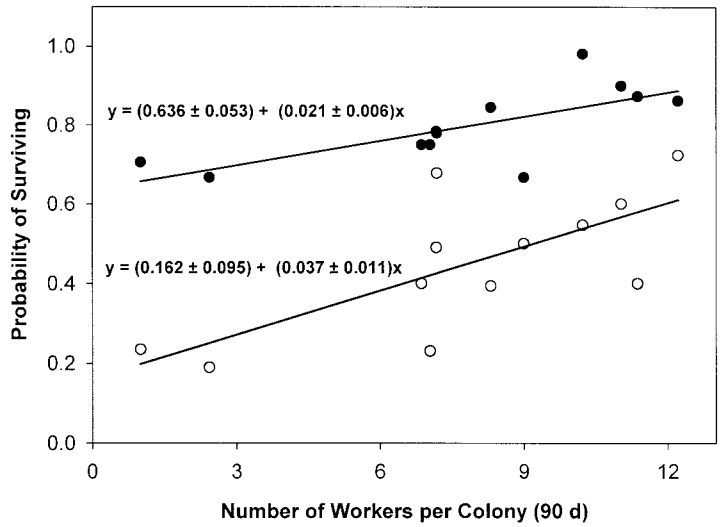

Fig. 3. Correlation between probability of survival of Formosan subterranean termite colonies from 90 to 180 d (filled circles) and 90–360 d (open circles) of age and mean number of workers per colony at 90 d of colony age, showing regression lines.

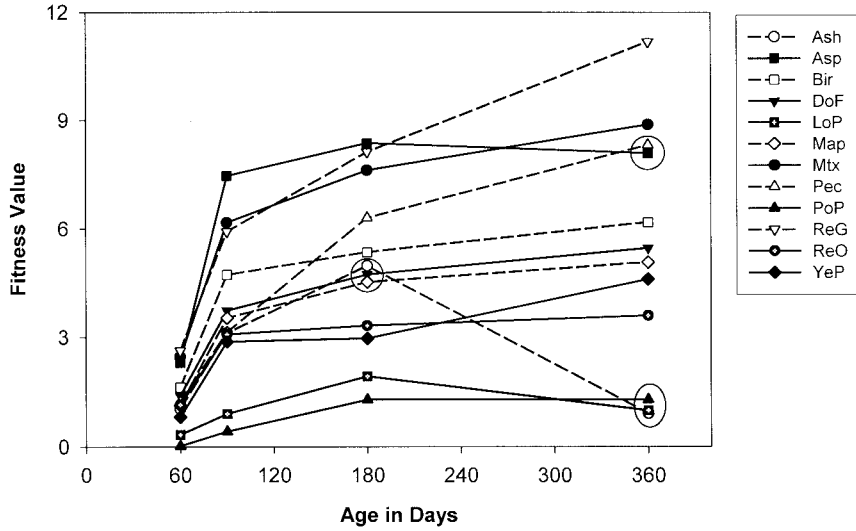

Fig. 4. Fitness values calculated as the product of number of workers + soldiers and probability of survival of Formosan subterranean termite incipient colonies fed on 11 wood species and a nutritionally supplemented matrix. Encircled data points are not significantly different ($\alpha = 0.05$) after Student *t*-test.

Analyses showed that food treatment had a significant effect on colony growth and progeny survival. This is evidence that different species of wood provide Formosan subterranean termites with different nutritional value. Differences in nutritional quality may be a result of the presence of essential nutrients in higher quantities or reduced concentrations of deleterious chemicals.

Colony survival was affected by wood species indirectly by affecting progeny survival. Analyses showed that colonies surviving to 180 d had significantly more workers at 90 d than colonies that died before 180 d (Table 5). Similar differences were observed between 180 and 360 d of colony age. The analyses also showed that queen fecundity was affected only mildly by food treatment (Table 4). This indicates that the differences observed in colony growth among food treatments were mainly the result of differences in progeny survival. Progeny survival may be affected by the presence of toxic compounds in the food source or by cannibalism induced by nutritional deficiency.

Indications of a deficient nutrition were observed in colonies feeding on ponderosa pine, 75% of which showed both male and female reproductive lacking antennae. The lack of antennae may be because of biting and consumption by the other partner. This type of behavior may be an indication of some specific nutritional need. Missing antennae may contribute to deficient brood care and increase of progeny mortality.

The nutritionally supplemented matrix, red gum, aspen, and pecan provided the incipient colonies with the greatest growth and/or survival. Colonies feeding on these four treatments, except aspen, produced more workers and soldiers and had better progeny survival. Colony survival was high in the aspen and red gum treatments and average in the supplemented matrix and pecan treatments. Fitness values at 180 and 360 d of colony age were the greatest of these four treatments.

The treatments that showed the lowest fitness values were ponderosa pine and loblolly pine (Fig. 4). These low values resulted from low colony growth and survival. These two treatments also had the lowest estimated progeny survival to 180 d of colony age (Table 4). Observed correlation between the number of workers per colony and colony survival may explain the increase in colony mortality observed in the ponderosa pine treatment group.

In general, colonies fed with softwood species produced fewer progeny than that of colonies fed with hardwood species (Table 3). However, there were significant differences in colony growth and colony survival within the soft wood species treatments. Colonies fed on Douglas fir had significantly more workers and soldiers than colonies fed in ponderosa and loblolly pines at 90 d of age. At 180 d of age, however, these differences were significant only between the Douglas fir and ponderosa pine treatments and no differences were observed at 360 d of age. Still, colonies feeding in Douglas fir had greater fitness values than those feeding in loblolly pine and ponderosa pine at 180 and 360 d of age (Fig. 4), mainly because colonies feeding on Douglas fir had a significantly greater survival ($Z > 1.98$).

Colonies feeding on ash showed a sharp decline in fitness from 180 to 360 d of age mainly because of an increase in colony mortality during this period. Estimated progeny survival to 180 d of age was the second highest for the ash treatment (Table 4). Similar increased mortality was observed in the aspen treatment. This increase in mortality was not observed in any of the other treatments (Fig. 3).

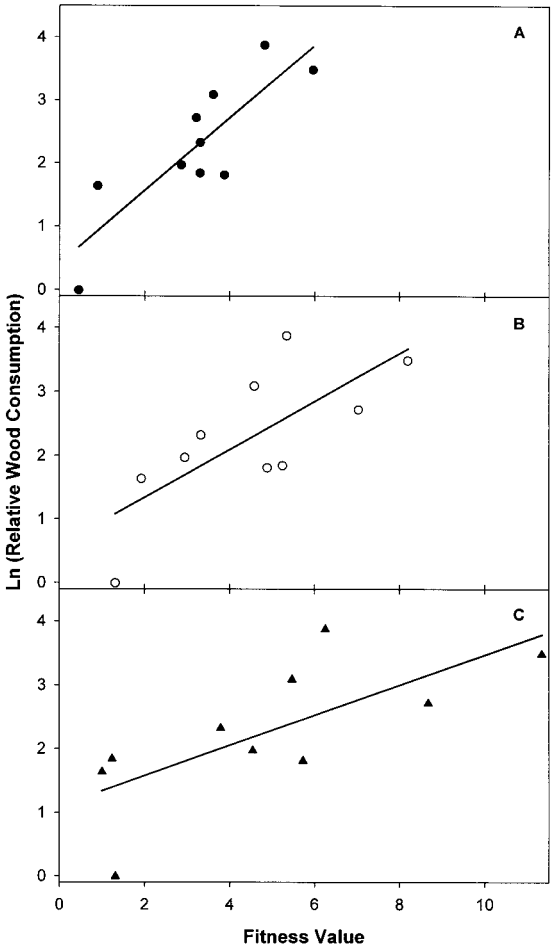

Fig. 5. Correlation between relative wood consumption by the Formosan subterranean termite in a choice test (Morales-Ramos and Rojas 2001) and fitness values of 90-d-old (A), 180-d-old (B), and 360-d-old (C) colonies. Lines represent regression models.

These results constitute strong evidence indicating that the quality of food source affects growth and survival of Formosan subterranean termite colonies and that the quality of food varies in different wood species. There was a significant correlation between the fitness value of Formosan subterranean termite colonies feeding in different wood species and preference of these wood species by the termites suggesting that nutritional value of the food may play a role in food preference. However, the low R^2 (0.42, 0.52, and 0.488) values observed indicate that Formosan subterranean termite feeding preferences are only partially determined by nutritional value of the food source. There are probably many other factors involved in Formosan subterranean termite feeding preferences that may be physical and chemical in nature. Continuing research in this topic may prove useful for improving baiting technology.

Acknowledgments

We thank Simone DeSonier and Patrick Plaisence for their valuable assistance building the nesting dishes.

References Cited

Beal, R. H. 1987. Introduction of *Coptotermes formosanus* Shiraki to the continental United States, pp. 48–53. *In* M. Tamashiro and N. Y. Su [eds.], Biology and control of the Formosan subterranean termite. Research and extension series 083, College of Tropical Agriculture and Human Resources, University of Hawaii, Honolulu, Hawaii.

Carey, J. R. 1993. Applied demography for biologists with special emphasis on insects. Oxford University Press, New York.

Edwards, R., and A. E. Mill. 1986. Termites in buildings. Rentokil Limited, Felcourt, East Grinstead, United Kingdom.

Emlen, J. M. 1973. Ecology: an evolutionary approach. Addison Wesley, Reading, MA.

Grace, J. K., H. M. Tome, T. G. Shelton, R. J. Oshiro, and J. R. Yates III. 1996. Baiting studies and considerations with *Coptotermes formosanus* (Isoptera: Rhinotermitidae) in Hawaii. Sociobiology 28: 511–520.

Henderson, G., and B. T. Forschler. 1996. Termite bait screening using naturally infested trees, pp. 449–458. *In* K. B. Widley [ed.], Second International Conference on Insect Pests in the Urban Environment. Heriot-Watt University, Edinburgh, Scotland.

Higa, S. Y. 1981. Flight colony foundation, and development of the gonads of the primary reproductives of the Formosan subterranean termite, *Coptotermes formosanus* Shiraki. Ph.D. dissertation, University of Hawaii, Honolulu, HI.

King, E. G., and W. T. Spink. 1974. Laboratory studies of the biology of the Formosan subterranean termite with primary emphasis on young colony development. Ann. Entomol. Soc. Am. 67: 953–958.

King, E. G., and W. T. Spink. 1975. Development of incipient Formosan subterranean termite colonies in the field. Ann. Entomol. Soc. Am. 68: 355–358.

Mannesmann, R. 1973. Comparison of twenty-one commercial wood species from North America in relation to feeding rates of the Formosan termite, Coptotermes formosanus Shiraki. Mater. Org. 8: 107–120.

Ott, L. 1984. An introduction to statistical methods and data analysis, 2nd ed. Duxbury Press, Boston, MA.

Manly, B.F.J. 1976. Extension to Kiritani and Nakasuji's method for analyzing insect stage-frequency data. Res. Popul. Ecol. 17: 191–199.

Morales-Ramos, J. A., and M. G. Rojas. 2001. Nutritional ecology of the Formosan subterranean termite (Isoptera: Rhinotermitidae): feeding response to commercial wood species. J. Econ. Entomol. 94: 516–523.

Roff, D. A. 1992. The evolution of life histories: theory and analysis. Chapman & Hall, New York.

Rojas, M. G., J. A. Morales-Ramos, and E. G. King. 1999. Response of *Catolaccus grandis* (Hymenoptera: Pteromalidae) to its natural host after ten generations of rearing on a factitious host Callosobruchus maculatus (Coleoptera: Bruchidae). Environ. Entomol. 28: 137–141.

Rojas, M. G., and J. A. Morales-Ramos. 2001. Bait matrix for delivery of chitin synthesis inhibitors to the Formosan subterranean termite (Isoptera: Rhinotermitidae). J. Econ. Entomol. 94: 506–510.

SAS Institute. 1995. JMP statistics and graphics guide, version 3 of JMP. SAS Institute, Cary, NC.

Smythe, R. V., and F. L. Carter. 1970. Feeding responses to sound wood by *Coptotermes formosanus*, Reticulitermes flavipes, and *R. virginicus* (Isoptera: Rhinotermitidae). Ann. Entomol. Soc. Am. 63: 841–847.

Su, N. Y. 1991. Evaluation of bait-toxicants for suppression of subterranean termite populations. Sociobiology 19: 211–220.

Su, N. Y., and R. H. Scheffrahn. 1990. Economically important termites in the United States and their control. Sociobiology 17: 77–94.

Su, N. Y., and R. H. Scheffrahn. 1993. Laboratory evaluation of two chitin synthesis inhibitors, hexaflumuron and diflubenzuron, as bait toxicants against Formosan and eastern subterranean termites (Isoptera: Rhinotermitidae). J. Econ. Entomol. 86: 1453–1457.

Su, N. Y., and R. H. Scheffrahn. 1996. Comparative effects of two chitin synthesis inhibitors, hexaflumuron and lufenuron, in a bait matrix against subterranean termites (Isoptera: Rhinotermitidae) J. Econ. Entomol. 89: 1156–1160.

Su, N. Y., and M. Tamashiro. 1987. An overview of the Formosan subterranean termite (Isoptera: Rhinotermitidae) in the world, pp. 3–15. *In* M. Tamashiro and N. Y. Su [eds.], Biology and control of the Formosan subterranean termite. Research and extension series 083, College of Tropical Agriculture and Human Resources, University of Hawaii, Honolulu, Hawaii.

Tukey, J. W. 1958. Bias and confidence in not quite large samples. Ann. Math. Stat. 29: 614.

Waller, D. A., C. G. Jones, and J. P. La Fage. 1990. Measuring wood preference in termites. Entomol. Exp. Appl. 56: 117–123.

Woodson, W. D., B. A. Wiltz, and A. R. Lax. 2001. Current distribution of the Formosan subterranean termite (Isoptera: Rhinotermitidae) in the United States. Sociobiology 37: 661–671.

Received for publication 26 January 2002; accepted 22 September 2002.